

NEW COMBINATIONS IN *SETARIA* (POACEAE: PANICEAE)

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ABSTRACT

Setaria subgenus *Reverchoniae* is proposed. New combinations in subgenus *Reverchoniae*, *Setaria reverchonii* (Vasey) Pilg. subsp. *ramiseta* (Scribn.) W.E. Fox, *S. reverchonii* (Vasey) Pilg. subsp. *firmula* (Hitchc. & Chase) W.E. Fox are proposed. New combinations in subgenus *Paurochaetium*, *S. utowanaea* (Scribn.) Pilg. var. *ophiticola* (Hitchc. & Ekman) W.E. Fox, *S. utowanaea* (Scribn.) Pilg. var. *subtransiens* (Hitchc. & Ekman) W.E. Fox are also proposed. Keys separating the subgenera, subspecies of *S. reverchonii*, species of subgenus *Paurochaetium*, and varieties of *S. utowanaea* are included.

RESUMEN

Se propone *Setaria* subgénero *Reverchoniae*. Son propuestas combinaciones nuevas en el subgénero *Reverchoniae*, *S. reverchonii* (Vasey) Pilg. subsp. *ramiseta* (Scribn.) W.E. Fox y *S. reverchonii* (Vasey) Pilg. subsp. *firmula* (Hitchc. & Chase) W.E. Fox,. Son también propuestas combinaciones nuevas en el subgénero *Paurochaetium*, *S. utowanaea* (Scribn.) Pilg. var. *ophiticola* (Hitchc. & Ekman) W.E. Fox y *S. utowanaea* (Scribn.) Pilg. var. *subtransiens* (Hitchc. & Ekman) W.E. Fox. Se incluyen claves para separar los subgéneros, subspecies de *S. reverchonii* y las variedades de *S. utowanaea*.

INTRODUCTION

Setaria P. Beauv. is a cosmopolitan genus important in cultivated crops [*S. italica* (L.) P. Beauv.], perennial forage grasses [*S. macrostachya* H.B.K.] and noxious weeds [*S. viridis* (L.) P. Beauv.].

Setaria (Poaceae:Paniceae) is one of several genera closely related to *Panicum*. Tribal and generic arrangement of the species of the Poaceae as classified by Häckel (1887) has been revised by Prat (1936), Pilger (1954), Stebbins (1956), Clayton and Renvoize (1986) and Soderstrom (1986). However, the circumscription of the Paniceae has remained rather stable. For additional discussion of previous work see Fox (1999). Most taxa in *Setaria* can be easily differentiated from its closest relatives *Panicum* and *Paspalum* by the presence of bristles subtending the spikelets, these representing modified inflorescence branches.

Rominger (1962) monographed the species of *Setaria* from North America and classified 43 species occurring in three subgenera: *Ptychophyllum* (6 species), *Setaria* (27 species) and *Paurochaetium* (10 species). Twenty-five are native to North America, ten originate from South America and eight are from the Old World (Rominger 1962).

The subgenus *Paurochaetium* forms an "artificial group" (Rominger 1962) distinguished from the remainder of the genus by the occurrence of only one bristle usually below the terminal spikelet of the primary branches. The subgenus occurs as two separate complexes. The first complex ranges from southern Florida through the West Indies and into the Yucatan region of Mexico and Belize. The complex includes *Setaria distantiflora* (A. Richard) Pilg., *S. pradana* (Léon) Léon, *S. leonis* (Ekman) Léon, *S. ophiticola* (Hitchc. & Ekman) Léon, *S. subtransiens* Hitchc. & Ekman, *S. utowanaea* (Scribn.) Pilg., and *S. chapmanii* (Vasey) Pilg.. The second complex occurs from northeastern Mexico through the western two-thirds of Texas, into southern Oklahoma and west into New Mexico. It extends from the Balcones Escarpment of Texas to Chaves County, New Mexico. The complex includes *S. firmula* (Hitchc. & Chase) Pilg., *S. ramiseta* (Scribn.) Pilg. and *S. reverchonii* (Vasey) Pilg.. Not included in Rominger (1962) is the species *S. variifolia* (Swallen) G. Davidse found in the Yucatan Peninsula of Mexico and south.

Rominger (1962) separated the subgenus from the remainder of *Setaria* by the presence of a single bristle "usually" below the terminal spikelet of each primary branch. Gould (1975) used the same character to separate the species that occur in Texas; however, he reported a problem with the identification of specimens based on this character. These problems led to the current research in the subgenus.

The objectives of the research were to 1) determine the relationships of the taxa in the Texas/Mexico/Oklahoma/New Mexico complex and 2) provide a taxonomic treatment of all taxa recognized by Rominger (1962) in the subgenus *Paurochaetium* and *S. variifolia*.

MATERIALS AND METHODS

Field collections were made during the flowering periods of the species throughout Texas, Florida and Belize. To insure isolation between the populations, a minimum distance of five miles was traveled between successive collection sites. Ten independent specimens from each site were semi-randomly collected and pressed; selection was biased in favor of mature plants that did not show any signs of damage from insects, herbivores, trampling, etc. The West Indies species were studied from herbaria specimens. In some cases sufficient samples were available of a single collection to serve as a "real" population. In others, "artificial" populations were created based upon similar geographic location. A total of 78 populations were studied for the subgenus.

Table 1 lists the 52 characters measured from representative populations to determine the relationship between the 11 species. All characters of selected populations were measured and statistically analyzed to determine significant characters for the detailed study of the subgeneric relationships. Nineteen characters were determined to be significant and included in that analysis. The following hypothesis was tested: taxa of subgenus *Paurochaetium* should be classified in one subgenus versus the need to describe a new subgenus. Two hundred and ninety two operational taxonomic units (OTU's), representing all species included in the study, were measured.

Univariate statistics (mean, standard deviation and range) were obtained using the PSI-Plot software package (Poly Software International 1996). Multivariate statistics of principal component analysis (PCA) was obtained using the NT-SYS software package (Rohlf 1990). Principal components were derived using correlation matrices.

RESULTS AND DISCUSSION

SUBGENERIC STUDY

Based upon the analysis of the 11 species classified in *Setaria* subgenus *Paurochaetium*, two distinctly separate entities were discovered. These differences matched the two complexes within subgenus *Paurochaetium* mentioned earlier. Figure 1 illustrates the separation between the two complexes.

Based upon the relationships revealed through the PCA, geographical separation, consistent morphological differences and similar habitat requirements of the complexes, the subgenus *Reverchoniae* is proposed.

***Setaria* subgenus *Reverchoniae* W.E. Fox, subgenus nov.** BASIONYM: *Panicum reverchonii* Vasey, Bull. U.S. Dept. Agric. Div. Bot. 8:25. 1889. TYPE: *Reverchon s.n.* (US!). TYPUS: *Setaria reverchonii* (Vasey) Pilg.

Setaria subgeneris *Reverchoniae* ab subgeneri *Paurochaetio* per absentiam paleae flosculi inferior, paniculam erectam, spiculam grandiore (2.1–4.5 mm long, 1.2–2.6 mm latam) fortuito dispositam (non dispositam), atque axe inflorescentiae scabro differt.

Setaria subgenus *Reverchoniae* differs from subgenus *Paurochaetium* in the absence of a palea of the lower floret, erect panicle, larger spikelets (2.1–4.5 mm long, 1.2–2.6 mm wide) that are randomly disposed (not distichous), and the scabrous axis of the inflorescence.

Setaria subgenus *Reverchoniae* contains three taxa previously classified in the subgenus *Paurochaetium* (Rominger 1962) including the proposed subspecies: *Setaria reverchonii* (Vasey) Pilg. subsp. *reverchonii*, *S. reverchonii* (Vasey) Pilg. subsp. *ramiseta* (Scribn.) W.E. Fox and *S. reverchonii* (Vasey) Pilg. subsp. *firmita* (Hitchc. & Chase) W.E. Fox. *Setaria variifolia* was included in the subgenus, but was not treated originally by Rominger (1962). The lack of a palea in the lower floret best circumscribes the subgenus *Reverchoniae*

TABLE 1. Fifty-two characters used to assess morphological and reproductive variation in *Setaria* subgenus *Paurochaetium*. All characters were measured for quantitative variation except those labeled as TS [two-state (binary)] and MS [multi-state qualitative]. Italicized characters were found as significant and used in the final analysis.

Vegetative: *growth habit* (MS), *culm height*, culms branched/unbranched (BS), internodes hollow/solid (BS), node pubescence present/absent (BS), leaves basal/throughout (BS), leaf sheath pubescence present/absent (BS), leaf sheath pubescence length (if present), *leaf length*, *leaf width* (widest point), *leaf base width*, *leaf involt/ not involt* (BS), leaf pubescence abaxial present/absent (BS), leaf pubescence adaxial present/absent (BS), leaf pubescence margin present/absent (BS), collar pubescence present/absent (BS), collar pubescence length (if present), auriculate trichomes present/absent (BS), *auriculate pubescence length* (if present), *ligule type* (MS), *ligule length*

Inflorescence: *inflorescence length*, inflorescence axis pubescence present/absent (BS), distance between lower primary branches, distance between upper primary branches, terminal bristle length lowest branch, terminal bristle length upper primary branches, terminal bristle length terminal primary branch, bristle exceeding spikelet lowest branch (BS), bristle exceeding spikelet upper branch (BS), bristle exceeding spikelet terminal branch (BS)

Spikelet: *spikelet length*, *spikelet width*, *lower glume clasping* (BS), lower glume apex shape, lower glume # of veins (MS), *lower glume length*, upper glume equal/not equal fertile lemma, *upper glume length*, lower glume # veins (MS), sterile lemma equal/not equal fertile lemma (BS), *sterile lemma length*, sterile lemma # veins (MS), sterile palea present/absent (BS), *sterile palea length*, fertile lemma rugose (BS), *fertile lemma length*, *fertile palea length*, *caryopsis length*, *caryopsis width*, filament length, *anther length*, anther width

(exception *S. variifolia* that shares other characters aligning it with the subgenus). None of the members of subgenus *Reverchoninae* are sympatric with subgenus *Paurochaetium*. For further detail of the relationships of the two subgenera refer to Fox (1999).

KEY TO SUBGENERA OF *SETARIA*

1. Bristles one to many below each spikelet (some without bristles); leaf blades plicate 2
2. Leaf blades plicate; bristles present below only some of the spikelets *Ptychophyllum*
2. Leaf blades not plicate; bristles below all spikelets (rarely missing) *Setaria*
1. Bristles present usually only below the terminal spikelet of branch as an extension of branch; leaf blades not plicate 3
3. Panicles nodding (except *S. pradana*), bearing remote, appressed, mostly racemose branches with spikelets two ranked on an undulating axis; central inflorescence axis glabrous; palea of lower florets present and conspicuous *Paurochaetium*
3. Panicles erect; spikelets arranged randomly on branch; central inflorescence axis scabrous; palea of lower florets absent (except *S. variifolia*) *Reverchoninae*

SUBGENUS *REVERCHONINAE*

Four taxa are classified in the subgenus *Reverchoninae*: *Setaria reverchonii* subsp. *reverchonii*, *S. reverchonii* subsp. *ramiseta*, *S. reverchonii* subsp. *firmula* and *S. variifolia*. Figure 2 illustrates the relationship of the taxa in *Reverchoninae*.

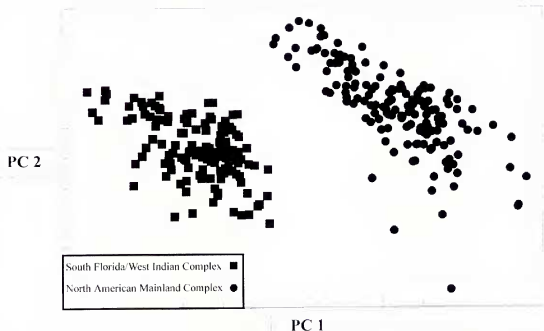


FIG. 1. Two-dimensional representation of all populations measured for the genus *Setaria* subgenus *Panrochaetium* (Rominger 1962).

Rominger (1962) classified *S. reverchonii*, *S. ramiseta*, and *S. firmula* as separate species following the combinations proposed by Pilger (1940). Other authors who have classified these taxa as species include Hitchcock (1935), Silveus (1942), Hitchcock (1951) and Gould (1975). When using the keys prepared by these authors, it becomes evident that the characters used do not result in consistent identifications. This problem resulted in the study of this complex and the following combinations.

***Setaria reverchonii* (Vasey) Pilg. subsp. *ramiseta* (Scribn.) W.E. Fox, comb. nov.** BASIONYM: *Panicum ramisetum* Scribn., Circ. U.S. Dept. Agric. Agrost. 27:9. 1900. *Setaria ramiseta* (Scribn.) Pilg., Engler & Prantl, Die Nat. Pflanzenf. 14e:72. 1940. TYPE: *G. Nealley* s.n. (LECTOTYPE: US!, by Rominger 1962).

Panicum subspicatum Vasey, Bull. U.S. Dept. Bot. 8:25. 1889, non *Panicum subspicatum* Desv., Opusc. Sci. Phys. Nat. 84. 1831.

Additional references and illustrations.—Hitchcock & Chase, Contr. U.S. Natl. Herb. 15:24, fig. 5. 1910; Hitchcock, Man. Grasses U.S. 611, fig. 1271. 1935.

***Setaria reverchonii* (Vasey) Pilg. subsp. *firmula* (Hitchc. & Chase) W.E. Fox, comb. nov.** BASIONYM: *Panicum firmulum* Hitchc. & Chase, Contr. U.S. Natl. Herb. 15:27, fig. 9. 1910. *Setaria firmula* (Hitchc. & Chase) Pilg. in Engler & Prantl, Die Nat. Pflanzenf. 14e:72. 1940. TYPE: *D. Griffiths* 6446 (HOLOTYPE: US!)

Additional references and illustrations.—Additional reference and illustration: Hitchcock, Man. Grasses U.S. 612, fig. 1273. 1935.

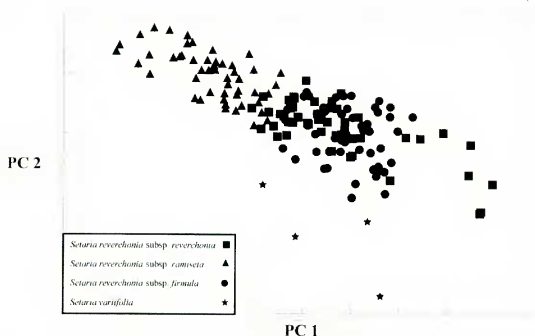


FIG. 2. Two-dimensional representation illustrating the relationships of the taxa described in *Setaria* subgenus *Reverchoninae*.

Setaria reverchonii subsp. *ramiseta* can be separated from the other taxa of the subgenus *Reverchoninae* with a shorter culm length, shorter penultimate leaf length, narrower leaf width, shorter second glume, shorter upper and lower lemma and shorter palea of the upper floret. *Setaria reverchonii* subsp. *reverchonii* is separated from subsp. *firmula* by a longer, narrower and usually involute leaf blade, a narrower leaf blade base above the collar and a longer lemma of the lower floret. Further references to the subspecies can be found in Fox (1999).

KEY TO SUBGENUS *REVERCHONINAE*

1. Palea of lower florets present and well developed; palea of upper (fertile) florets 3.0–3.1 mm long; distribution Yucatan peninsula of Mexico and Central America *S. variifolia*
1. Palea of lower florets absent or rudimentary; palea of upper florets (1.0–)1.8–2.5(–3.1) mm long; distribution Texas, New Mexico, Oklahoma and northern Mexico 2
2. Spikelets (2.4–)2.7–2.8(–3.4) mm long, (1.1–)1.5–1.6(–1.9) mm wide; second glumes (1.9–)2.4–2.5(–3.1) mm long; lemma of lower florets (1.0) 2.3–2.5(–3.2) mm long; lemma of upper florets (1.0–)2.2–2.3(–2.9) mm long; penultimate leaf blades (3.0–)6.8–7.6(–12.1) cm long; panicles (3.7) 17.7–20.7(–38.1) cm long *S. reverchonii* subsp. *ramiseta*
2. Spikelets (2.9–)3.2–3.4(–4.0) mm long, (1.2–)1.8–2.0(–3.6) mm wide; second glumes (2.4–)2.8–3.0(–3.6) mm long; lemma of lower florets (1.4) 2.8–3.0(–3.7) mm long; lemma of upper florets (2.2–)2.7–2.9(–3.4) mm long; penultimate leaf blades (3.6–)7.9–13.3(–28.6) cm long; panicles (9.5) 25.3–32.6(–64.8) cm long 3

3. Penultimate leaf blades (3.6–)11.7–13.3(–28.6) cm long, (1.4–)2.1–2.3(–3.4) mm wide, involute; leaf blade bases above collar (0.7–)1.3–1.5(–2.1) mm wide; lemma of lower florets (1.4–)2.9–3.0(–3.7) mm long *S. reverchonii* subsp. *reverchonii*
3. Penultimate leaf blades (5.1–)7.9–8.8(–15.4) cm long, (2.7–)4.4–4.7(–9.2) mm wide, flattened; leaf bases above collar (1.4–)3.0–3.2(–5.3) mm wide; lemma of lower florets (1.9–)2.8–2.9(–3.2) mm long *S. reverchonii* subsp. *firmula*

SUBGENUS *PAUROCHAETIUM*

The remaining seven taxa are retained the subgenus *Paurochaetium* as described by Rominger (1962). These include the original species of *Setaria distantiflora*, *S. leonis*, *S. ophiticola*, *S. pradana*, *S. subtransiens*, *S. utowanaea* and *S. chapmanii*. Taxonomic interpretation was difficult in the subgenus *Paurochaetium* due to a small sample size. Unfortunately, few specimens have been collected over time and available for the study. Hitchcock (1936) and Rominger (1962) classified *S. utowanaea*, *S. ophiticola* and *S. subtransiens* as distinct species. However, based upon the specimens examined in this study the following combinations are proposed.

Setaria utowanaea (Scribn.) Pilg. var. *ophiticola* (Léon) W.E. Fox, comb. nov. BASIONYM: *Panicum ophiticola* Hitchc. & Ekman ex Hitchcock, U.S. Dept. Agric. Misc. Publ. 243:293, fig. 282. 1936. *Setaria ophiticola* (Hitchc. & Ekman) Léon in Fl. Cuba 163. 1946. TYPE: *E.L. Ekman* 12712 (HOLOTYPE: US!).

Setaria utowanaea (Scribn.) Pilg. var. *subtransiens* (Hitchc. & Ekman) W.E. Fox, comb. nov. BASIONYM: *Panicum subtransiens* Hitchc. & Ekman ex Hitchcock, U.S. Dept. Agric. Misc. Publ. 243:351, fig. 323. 1936. TYPE: *E.L. Ekman* 16828 (HOLOTYPE: US!).

Based upon the mid-leaf width, leaf base width, spikelet length, lower lemma length and palea length of the upper floret, the varieties of *Setaria utowanaea* are classified separately from the remainder of subgenus *Paurochaetium*. Figure 3 illustrates the relationship of the three taxa in the *Setaria utowanaea* complex. *Setaria utowanaea* var. *subtransiens* differs from the other members of the species with a single bristle present below most spikelets on the branch, bristle length exceeding the spikelet, and spikelet width. *Setaria utowanaea* var. *utowanaea* is separated from *S. utowanaea* var. *ophiticola* by blade length, spikelet width, lack of tufted basal leaves and the presence of involute leaves on the upper culm. *Setaria utowanaea* var. *ophiticola* has shorter leaf blades, narrower spikelets, a tufted lower leaf arrangement and upper leaves that are slightly folded or flat. The following key separates the species of subgenus *Paurochaetium*. A key to separate the varieties of *Setaria utowanaea* will follow. Further reference to the taxa of subgenus *Paurochaetium* can be found in Fox (1999).

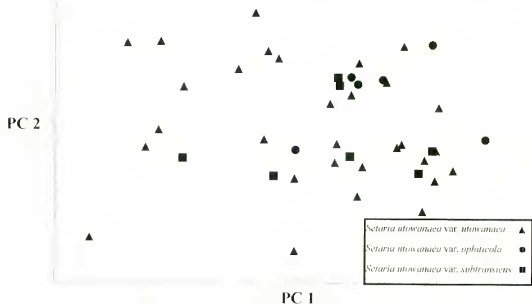


FIG. 3. Two-dimensional representation of the relationship between *Setaria utowanaea* var. *utowanaea*, *S. utowanaea* var. *ophiticola* and *S. utowanaea* var. *subtransiens*.

KEY TO SUBGENUS PAUROCHAETUM

1. Spikelets (1.8–)2.0–2.2(–2.4) mm long, (1.0–)1.1–1.2(–1.3) mm wide, ovate, lacking palea of lower florets; penultimate leaf blades (9.3–)15.1–19.1(–34.4) cm long, (2.3–)3.2–3.9(–7.7) mm wide; leaf blade bases above collar (1.1) 1.2–2.7(–6.0) mm wide; second glumes subequal to equal fertile lemmas *S. chapmanii*
1. Spikelets (1.3–)1.4–2.4(–2.5) mm long, paleas of lower floret conspicuously present; leaf blade bases above collar (0.3–)0.4–1.4(–1.8) mm wide; second glumes conspicuously shorter than fertile lemmas 2
2. Panicles erect; spikelets (1.7–)1.8–2.0(–2.5) mm long, spreading; lower lemmas (1.4–)1.6–1.8(–2.1) mm long; lower paleas (0.4–)0.8–1.1(–1.4) mm long; upper paleas (1.2–)1.3–1.5(–1.9) mm long *S. pradana*
2. Panicles subflexuous; spikelets (1.8–)2.2–2.4(–2.5) mm long [except *S. distantiflora* (1.3–)1.4–1.5(–1.7)], not spreading; lower lemmas (1.6–)1.9–2.2(–2.4) mm long; lower paleas (0.8–)1.2–1.8(–1.9) mm long; upper paleas (1.4–)1.6–1.9(–2.1) mm long 3
3. Spikelets (1.3–)1.4–1.5(–1.7) mm long; first glumes (0.4–)0.6–0.7(–0.9) mm long; second glumes (0.6–)0.9–1.1(–1.3) mm long; lower lemmas (1.1–)1.3–1.4(–1.5) mm long; palea of lower florets (0.3–)0.9–1.1(–1.3) mm long; palea of upper florets (0.9–)1.0–1.1(–1.3) mm long *S. distantiflora*
3. Spikelets (1.6–)1.8–2.4(–2.5) mm long; first glumes (0.6–)0.7–1.3(–1.4) mm long; second glumes (0.7–)1.2–1.7(–2.1) mm long; palea of lower florets (1.2–)1.6–2.2(–2.4) mm long; palea of upper florets (1.2–)1.4–1.9(–2.1) mm long 4
4. Penultimate leaf blades (3.6–)4.7–5.9(–7.4) mm wide; leaf blade base above collar (1.1–)1.3–1.5(–1.8) mm wide; spikelet (1.6–)1.8–2.0(–

- 2.3) mm long; lemma of lower florets (1.2-)1.6-1.8(-2.2) mm long;
 palea of upper florets (1.2-)1.4-1.5(-1.7) mm long *S. leonis*
 4. Penultimate leaf blades (0.9-)1.1-1.3(-4.2) mm wide; leaf blade above
 collar 0.4-1.3(-1.4) mm wide; spikelets (1.8-)2.2-2.4(-2.5) mm long;
 lemma of lower florets (1.6-)1.9-2.2(-2.4) mm long; palea of upper
 florets (1.4-)1.6-1.9(-2.1) mm long *S. utowanaea*

KEY TO VARIETIES OF *SETARIA UTOWANAEA*

1. Bristles present below most spikelets on branch, (2.5-)4.0-5.1(-6.4) mm
 long, exceeding spikelet *S. utowanaea* var. *subtransiens*
 1. Bristles present below only terminal spikelet of branch, (0.4-)0.5-3.3(-3.9)
 mm long, not exceeding spikelet 2
 2. Leaf blades (7.8-)13.1-16.0(-21.9) mm long; spikelets 0.7-0.8(-0.9) mm
 wide; basal leaves not tufted, upper leaves involute *S. utowanaea*
 var. *utowanaea*
 2. Leaf blades 3.3-5.4(-6.2) mm long; spikelets 0.5-0.7 mm wide; basal
 leaves tufted, upper leaves flat or slightly folded toward apex *S. utowanaea*
 var. *ophiticola*

CONCLUSIONS

Rominger (1962) stated that the separate classification of *Setaria* subgenus *Paurochaetium* is "artificial." However, based upon this study and input from various others, it is our opinion that, although "artificial" by definition, the eleven taxa form a distinct group distinguishable from the remainder of *Setaria*. Based upon this analysis, keys have been developed that consistently separate the taxa from the subgenera *Setaria* and *Ptychophyllum*.

However, our understanding of the relationships within what was originally classified as *Setaria* subgenus *Paurochaetium* have changed based upon these analyses. The proposal of the new subgenus, *Setaria* subgenus *Reverchoninae*, provides a natural separation of the original taxa recognized by Rominger (1962). With the proposal of the new subgenus, *Setaria* now has four recognized subgenera.

The inclusion of *Setaria variifolia* with the remainder of *Setaria* subgenus *Reverchoninae* added a little known taxon to the subgenera of *Setaria* that has a single bristle usually only below the terminal spikelet of the branch. Davidse (1981) suggested that *S. variifolia* was closely related to taxa of subgenus *Paurochaetium* as defined by Rominger (1962). This taxon provides a challenge to its classification due to the overlapping characteristics with several of the subgenera. However, based upon these analyses, the taxon is best classified with the subgenus *Reverchoninae*. *Setaria variifolia* warrants further study to determine if this classification is truly defined. A comparative analysis of all of the subgenera would determine if the classification is correct.

Within *Setaria* subgenus *Reverchoninae* two name combinations have been proposed. Based upon numerical study of morphology, leaf anatomy and

DNA content analyses *S. reverchonii* subsp. *firmula* and *S. reverchonii* subsp. *ramiseta* have been proposed (Fox 1999). The taxa of the subgenus (excluding *S. variifolia*) show a substantial amount of intergradation.

The remainder of the species originally classified by Rominger (1962) are retained in the subgenus *Paurochaetium*. However, name combinations have been proposed for two of the taxa, *S. utowanaea* var. *ophiticola* and *S. utowanaea* var. *subtransiens*.

There is a need for the study of the reproductive behavior of the three subspecies of *S. reverchonii*. The results of such research would help better understand the relationship of the taxa. If these taxa do not hybridize, it may indicate a trend towards speciation.

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